ANNOUNCEMENTS

- Hit *Record*! Unmute!
- Lab 1 graded, check comments
- Lab 3 not up yet, will be posted just before lab time on Weds
- First paper analysis due Friday (Strom et al. 2016 paper, on Canvas)

TURNOVER AND PRODUCTION

12 September 2022

LET'S TALK ABOUT PRODUCTION

- Where does the energy in aquatic food webs come from?

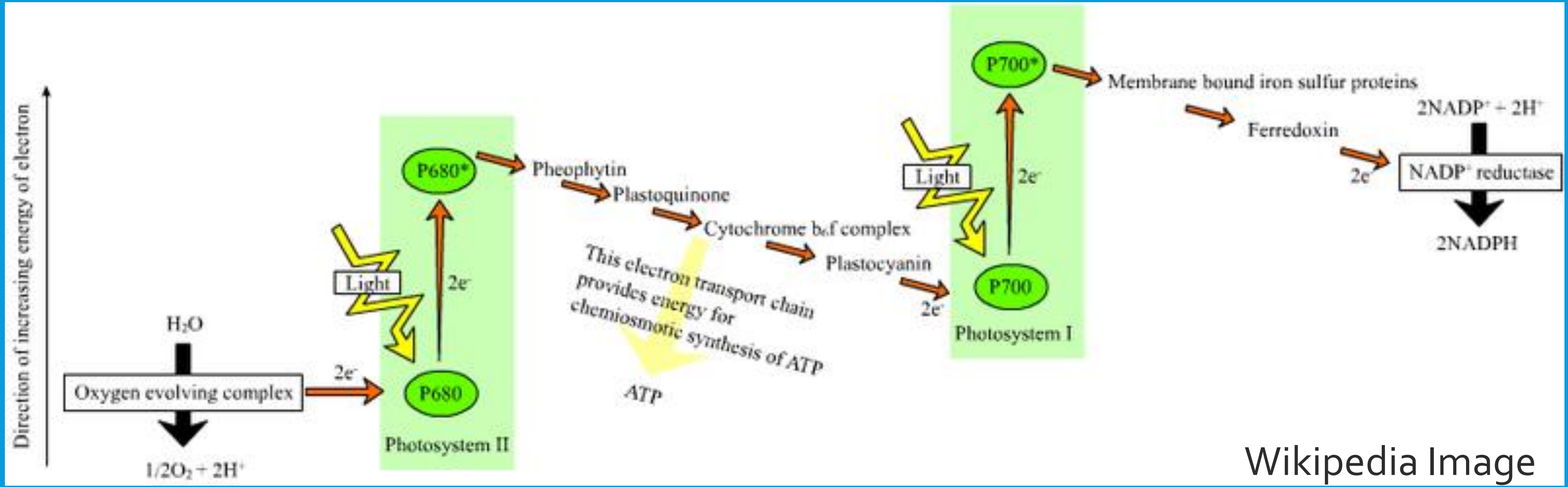
LET'S TALK ABOUT PRODUCTION

- Where does the energy in aquatic food webs come from?
  - Almost entirely solar energy (photosynthesis)
    - Take atmospheric Carbon, convert to carbohydrate
      - $CO_2 + 6H_2O \text{->} C_6H_{12}O_6 + 6O_2$ (glucose, in this example)
  - Chemosynthesis in deep sea vents
    - Still uses CO_2 as the Carbon source, but requires Hydrogen Sulfide oxidation instead of water
      - $CO_2 + 4H_2S + O_2 \text{->} CH_20 + 4S + 3H_2O$
      - Probably our last mention of chemosynthesis in this course.

GETTING CARBON FROM CO_2 USING SUN

- Z-Scheme:
  - Take water and light, free electrons by exciting photons
  - Ultimately yields 2 molecules of NADPH, also synthesizes ADP
    - NADPH: nicotinamide adenine dinucleotide phosphate
    - ATP: adenosine triphosphate
    - Collectively, cellular "energy currency"

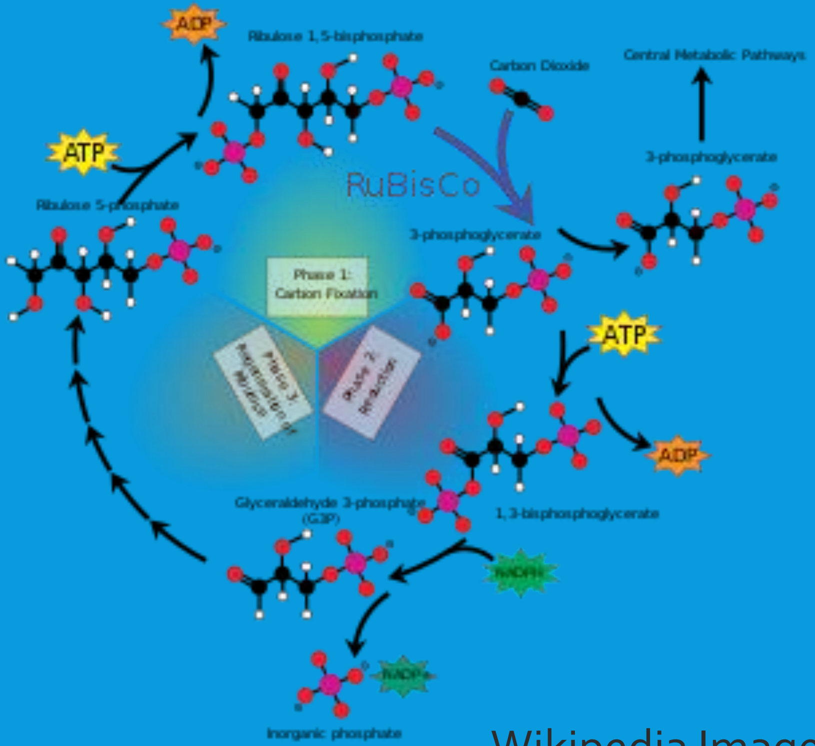
How do aquatic systems differ from terrestrial in availability?



Wikipedia Image

GETTING CARBON FROM CO_2 USING SUN

- Calvin Cycle:
  - Done without light!
  - Take ATP and NADPH from Z-Scheme, use enzyme RuBisCO to break bonds in CO_2
    - RuBisCO: Ribulose-1-5-bisphoshate carboxylase-oxygenase
  - Forms triose phosphate ($C_3H_5O_6P$)
    - AKA glyceraldehyde 3-phosphate
  - Most of triose phosphate recycled (hence Calvin "cycle") to make more RuBisCO
  - Some converted into simple carbohydrates (sugars) instead
    - $C_6H_{12}O_6$ (glucose) as a precursor, rapidly converted to other carbohydrates
      - glucose, sucrose, starch, cellulose, etc.
  - "Carbon fixation": Reduction (loss of electron) in converting CO_2 to sugars



Wikipedia Image

CARBON FIXATION PROCESSES

- C3 fixation: RuBisCO catalysis yields 3-Carbon glyceraldehyde 3-phosphate
  - 3-carbon intermediate product, Hence "C3"
- C4 fixation: PEP carboxylase catalysis yields 4-Carbon oxaloacetic acid as a first step. This intermediate product then "fed" to RuBisCO
  - 4-carbon intermediate product, Hence "C4"
  - Yields more carbon, therefore more sugar/carbohydrate
  - But more energetically expensive to make this extra sugar
    - Requires high light, high temperatures

So which mechanism do aquatic photosynthesizers likely use?

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  - Yields more carbon, therefore more sugar/carbohydrate
  - But more energetically expensive to make this extra sugar
    - Requires high light, high temperatures
  - As a result, algae and aquatic plants are almost all C3
    - Some novel evidence that cyanobacteria (blue-green algae) have C4 enzymes

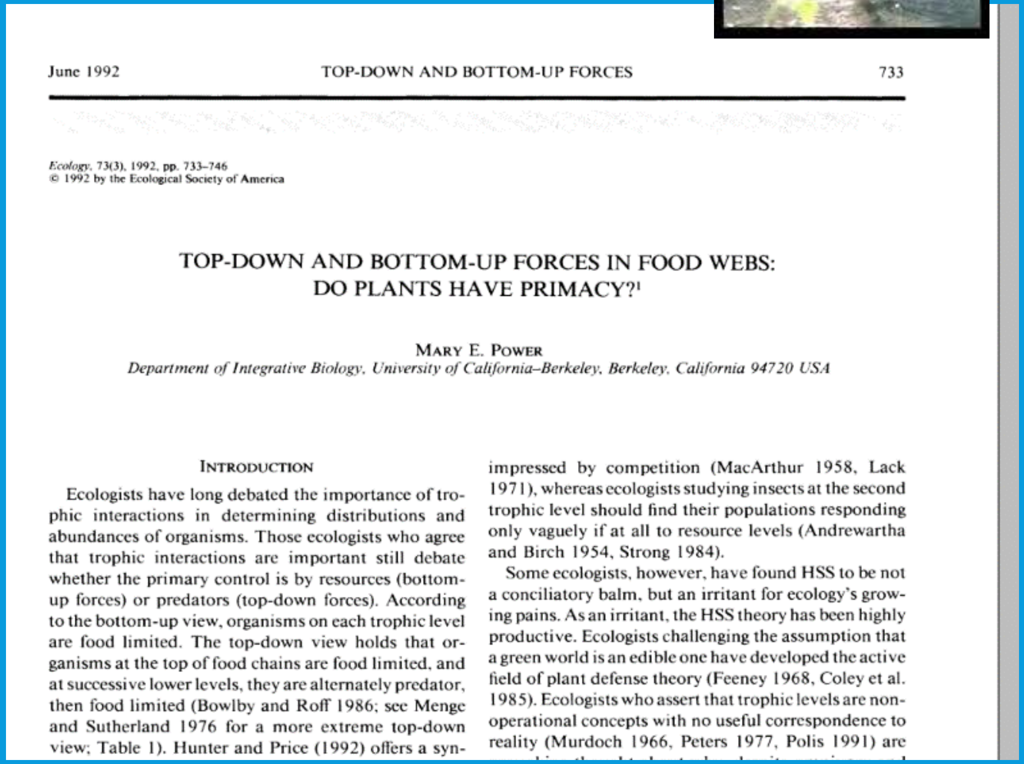
So which mechanism do aquatic photosynthesizers likely use?

WHY DO WE CARE ABOUT Z-SCHEMES AND CALVIN CYCLES IN FOOD WEBS?

- Longstanding debate in food web ecology: Top-down or bottom-up?
  - Top-down: Predators control producers
    - HSS from last lecture
  - Bottom-up: Producers control consumers
    - Therefore, sunlight controls the food web
    - "Food base" limits higher trophic levels.

- We'll return to this debate later in the course

- For now, let's assume plants and algae matter…



June 1992 TOP-DOWN AND BOTTOM-UP FORCES 733

Ecology, 73(3), 1992, pp. 733–746
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TOP-DOWN AND BOTTOM-UP FORCES IN FOOD WEBS: DO PLANTS HAVE PRIMACY?[1]

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Introduction

Ecologists have long debated the importance of trophic interactions in determining distributions and abundances of organisms. Those ecologists who agree that trophic interactions are important still debate whether the primary control is by resources (bottom-up forces) or predators (top-down forces). According to the bottom-up view, organisms on each trophic level are food limited. The top-down view holds that organisms at the top of food chains are food limited, and at successive lower levels, they are alternately predator, then food limited (Bowlby and Roff 1986; see Menge and Sutherland 1976 for a more extreme top-down view; Table 1). Hunter and Price (1992) offers a syn-

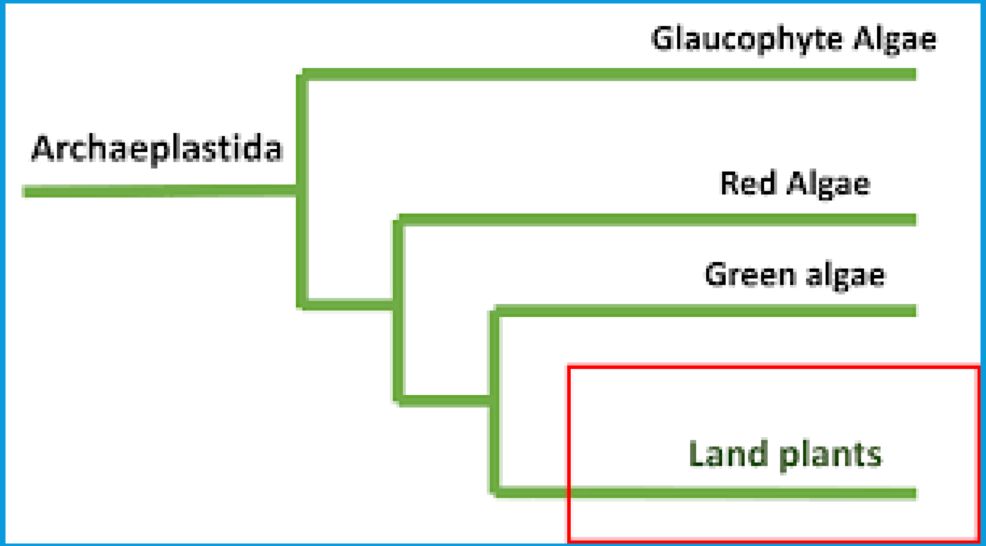
impressed by competition (MacArthur 1958, Lack 1971), whereas ecologists studying insects at the second trophic level should find their populations responding only vaguely if at all to resource levels (Andrewartha and Birch 1954, Strong 1984).

Some ecologists, however, have found HSS to be not a conciliatory balm, but an irritant for ecology's growing pains. As an irritant, the HSS theory has been highly productive. Ecologists challenging the assumption that a green world is an edible one have developed the active field of plant defense theory (Feeney 1968, Coley et al. 1985). Ecologists who assert that trophic levels are non-operational concepts with no useful correspondence to reality (Murdoch 1966, Peters 1977, Polis 1991) are

PRIMARY PRODUCERS

PRIMARY PRODUCERS

- Organisms that carry out primary production!
  - i.e., carry out photosynthesis
- In aquatic systems:
  - Algae (cyanobacteria, green algae, kelp, diatoms, etc.)
  - Plants (macrophytes, mosses, grasses, etc.)



All botanists are really just specialized phycologists…

SECONDARY PRODUCERS

SECONDARY PRODUCERS

- AKA Primary Consumers
- Organisms that eat primary consumers
  - Bacteria, fungi, invertebrates and vertebrates

SECONDARY CONSUMERS

- AKA Predators
- Organisms that eat secondary producers
  - Bacteria, fungi, invertebrates and vertebrates

The lines get blurry at this category

- Tertiary consumers eat secondary consumers, but also often eat secondary producers. And sometimes also eat primary producers…

PRIMARY PRODUCTION

- Generally represented as photosynthetic rate
- Mass or Carbon fixed per unit area per time
  - For example: grams C per m^3 per day

ECOSYSTEM METABOLISM

- GPP
- NEP
- ER

ECOSYSTEM METABOLISM

- GPP: Gross Primary Production
- NEP: Net Ecosystem Production
- ER: Ecosystem Respiration

- NEP = GPP – ER = Ecosystem metabolism

- Primary production from GPP is utilized and “lost” from the ecosystem via respiration (from consumers and from primary producers themselves)

ECOSYSTEM METABOLISM

- Autotrophic: NEP > 1
  - Ecosystem fixes more carbon than it uses
    - more photosynthesis-fixed Carbon than respiration
- Heterotrophic: NEP < 1
  - Ecosystem respires more carbon than it fixes
- How can an ecosystem be heterotrophic?

ECOSYSTEM METABOLISM

- Autotrophic: NEP > 1
  - Ecosystem fixes more carbon than it uses
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- Heterotrophic: NEP < 1
  - Ecosystem respires more carbon than it fixes
- How can an ecosystem be heterotrophic?
  - Relies on outside carbon sources ("allochthony")
    - Detritus inputs, particularly
    - Contrasts with "autochthony"
- Measurement of ecosystem metabolism tells you what food base ecosystem is relying upon

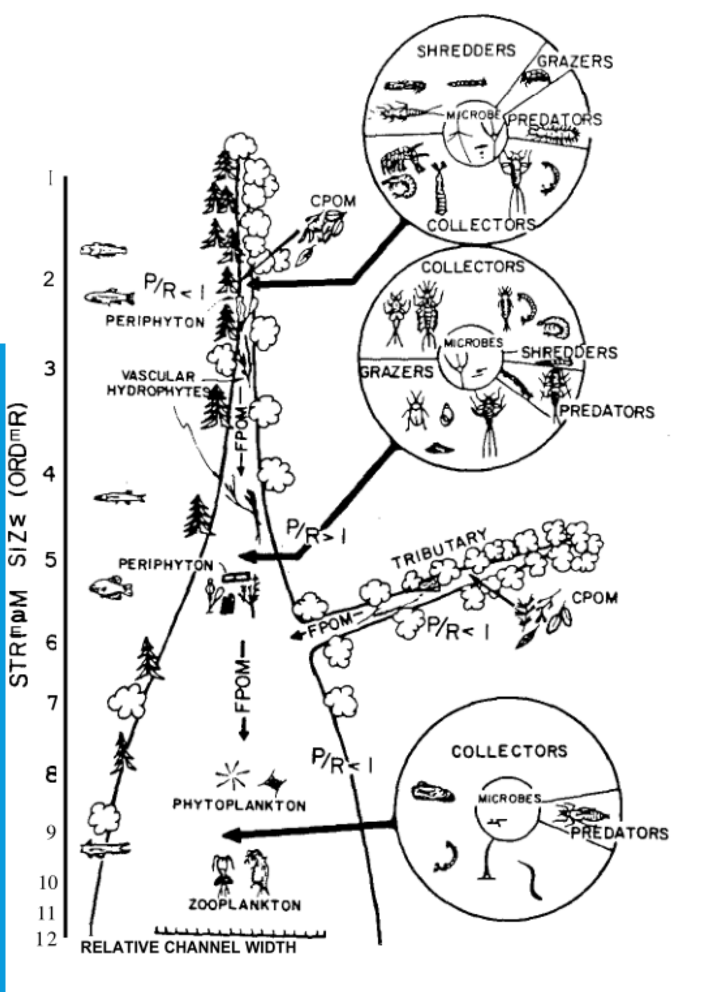


FIG. 1. A proposed relationship between stream size and the progressive shift in structural and functional attributes of lotic communities. See text for fuller explanation.

Figure from Vannote et al. (1980) *The River Continuum Concept*. The most famous figure in steam ecology

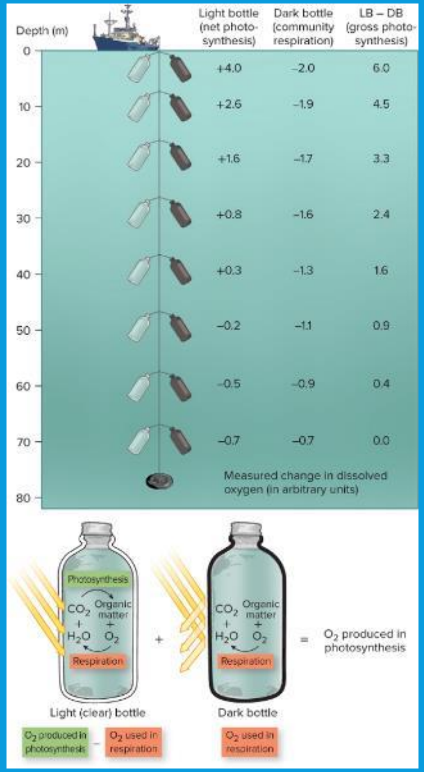
HOW DO WE MEASURE PRIMARY PRODUCTION?

(Specific to aquatic systems)

HOW DO WE MEASURE PRIMARY PRODUCTION?

(Specific to aquatic systems)

- Generally starts with measuring dissolved oxygen
- Bottle method: measure DO change in a "light bottle" and a "dark bottle"
- Field method: measure DO change over course of day(s)
- Light bottle = NEP (GPP – ER). Dark bottle = ER. Difference = GPP
- *In what situations would we choose one over the other?*



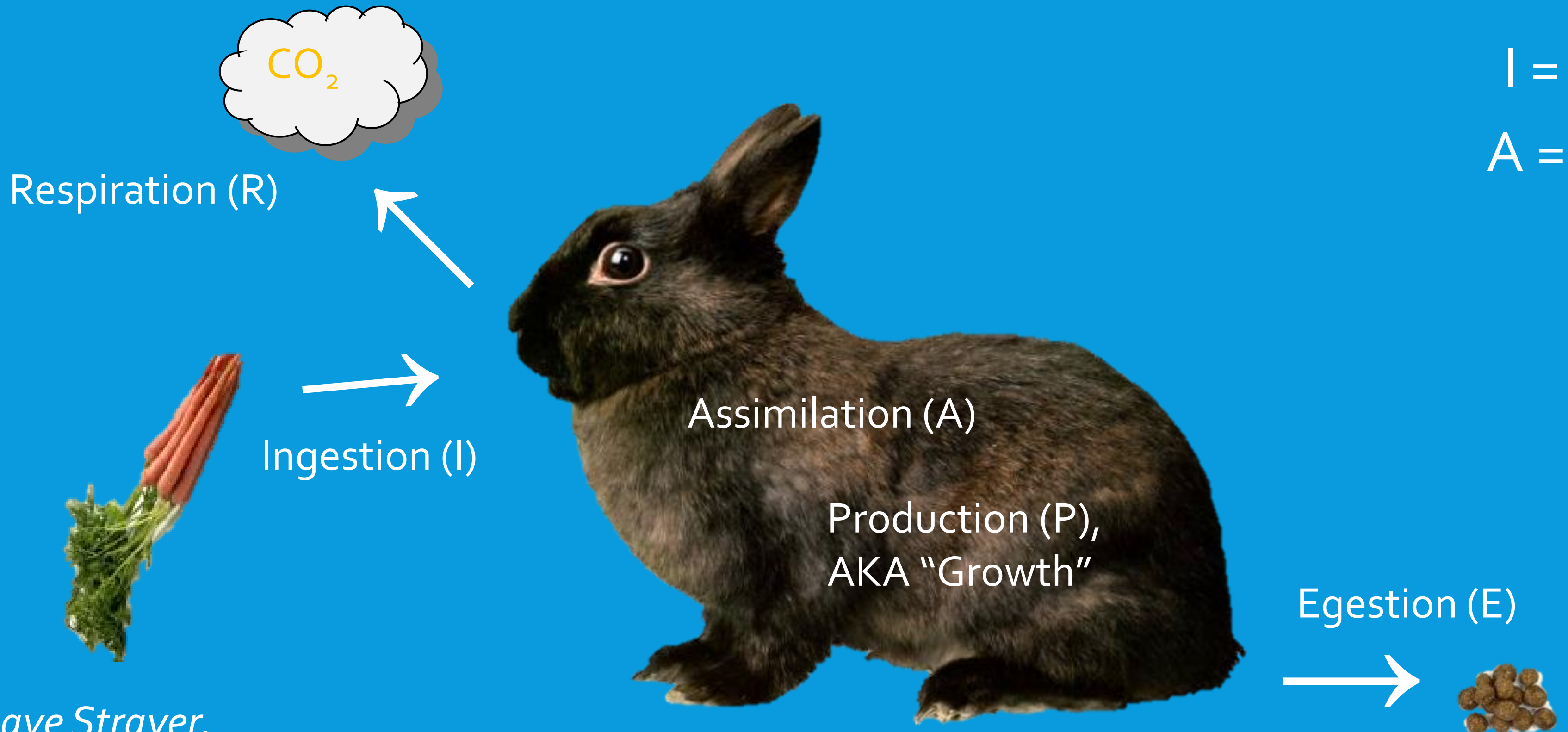
SECONDARY PRODUCTION

SECONDARY PRODUCTION

- Production ("growth") of all non-primary producing organisms in an ecosystem

$$I = A + E$$

$$A = R + P$$



Courtesy of Dave Strayer,
Cary Inst. Ecos. Studies (Ret.)

SO SECONDARY PRODUCTION IS JUST BIOMASS?

SO SECONDARY PRODUCTION IS JUST BIOMASS?

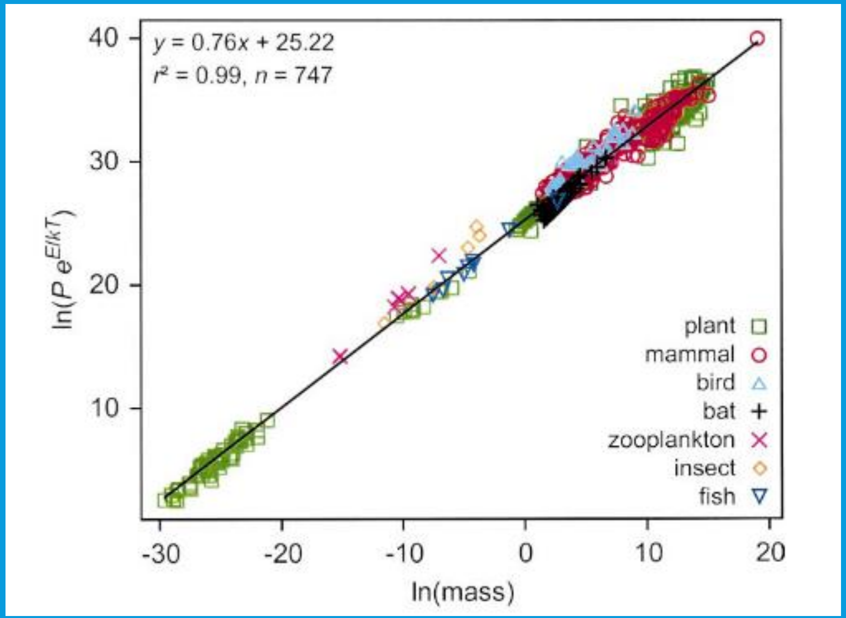
- No!
- Two are related, but biomass is only a part of secondary production
  - Also includes mortality, turnover, growth rate
  - Biomass can be eaten, leave the system.
- Secondary production at the individual level is *very* intensive. Generally calculated at the population level instead. Easier still to calculate at the community level (but still not easy)
- Turnover: We're talking specifically about biomass here (not species turnover)
  - Often expressed as a rate (e.g., how much biomass dies and becomes new biomass in a year)

CONTROLS ON SECONDARY PRODUCTION

CONTROLS ON SECONDARY PRODUCTION

- Similar to primary production
- Temperature (hotter = higher metabolism, generally)
- Organism size (bigger = higher metabolic rate, generally)

- Metabolic Theory of Ecology:
- Organism (or community, or ecosystem) metabolism scales with size according to a power law
- Kleiber's Law (1932): $I = I_0 M^{3/4}$
  - Where I is metabolic rate, M is biomass
  - Much debate over whether it is ¾ everywhere, in what cases



Brown et al. (2004) Ecology

MEASURING SECONDARY PRODUCTION

- Go out and weight some rabbits and collect their food and their poop?

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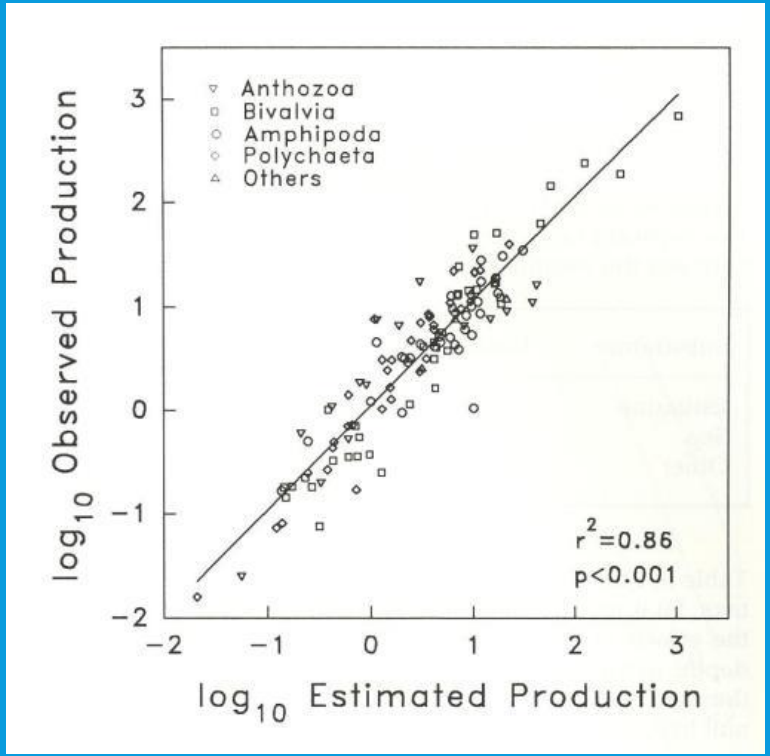
MEASURING SECONDARY PRODUCTION

- Go out and weight some rabbits and collect their food and their poop?
- Well, kinda!

- Alternative method: Use a model
- These tend to be terrible (log-log scale)
- If a ballpark estimate is all you need, these can work



Tumbiolo & Downing 1994

MEASURING SECONDARY PRODUCTION

- Go out and weight some rabbits and collect their food and their poop?
- Well, kinda!
- On the individual scale: In-depth measurements of growth rate, ingestion, egestion (very detailed, very hard)
- On the community scale: Can measure total growth of all organisms over time (easier, but not easy)
  - Per m^2 on a stream bed, or per m^3 of open water
  - Generally repeat measures, often seasonally
  - Get biomass, change in organism size, infer mortality. Often infer egestion/respiration.
  - Can get a mass balance over time, reasonable approximation for secondary production

SECONDARY PRODUCTION IN AQUATIC SYSTEMS

- Surprisingly, more known here than for terrestrial systems
  - “natural labs”, “closed systems”
- Secondary production tends to be large relative to primary production
  - Varies, but somewhere around 1/3-1/2 of organic inputs (autochthonous and allochthonous)
- Large secondary production values driven by turnover/recycling of biomass
  - Decomposers eat mostly consumers, not primary producers

TROPHIC BASIS OF PRODUCTION

- See Benke & Wallace (1980) paper for this lecture!

TROPHIC BASIS OF PRODUCTION

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- Application of secondary production
- Uses: 1) Annual production estimates (empirically, by weighing dried animals)
  2) Proportion of food categories consumed (empirically, by dissecting guts)
  3) Assimilation and production efficiencies (empirically, or from literature)
- Gives you an estimate of importance of food categories to the aquatic food web, amount of food needed from each food category (food limitation?)
- Very intensive, but can yield more interesting insight than gut contents or biomass alone

TABLE 5. Procedure for calculating production attributed to each food type and the amount of food type consumed for *Arctopsyche irrorata* (P = 605 mg m^{-2} yr^{-1}).

	Food type in foregut (%)		Assimilation efficiency* (AE)		Net production efficiency* (NPE)		Relative amount to production	Production attributed to food type (%)	Production attributed to food type ($mg \cdot m^{-2} \cdot yr^{-1}$)		Gross production efficiency* (AE × NPE)		Amount food type consumed ($mg \cdot m^{-2} \cdot yr^{-1}$)
Animal	73.1	×	.70	×	.5	=	25.6	93.3	564	÷	.35	=	1611
Vascular plant detritus	4.2	×	.10	×	.5	=	.21	0.8	5	÷	.05	=	100
Fine detritus	17.9	×	.10	×	.5	=	.90	3.3	20	÷	.05	=	400
Filamentous algae	2.0	×	.30	×	.5	=	.30	1.1	7	÷	.15	=	47
Diatoms	2.9	×	.30	×	.5	=	.44	1.6	10	÷	.15	=	67

* Based upon literature values; see text.

MORE EQUATIONS!

- We've talked about recycling/turnover. That only works if energy is highly conserved within a community. In other words, if ingestion efficiency is high.
- $P = (S - L)\,\varepsilon_g/(1 - \varepsilon_g)$
  - P = Secondary production
  - S = Supply of organic matter
  - L = Loss of organic matter (not including respiration)
  - ε_g = ingestion efficiency
- Ingestion efficiency value turns out to matter a lot
- If $\varepsilon_g > 0.5$, secondary production can *exceed* primary production

Strayer (2022) in Fundamentals of Ecosystem Science
DOI: 10.1016/B978-0-12-812762-9.00003-4

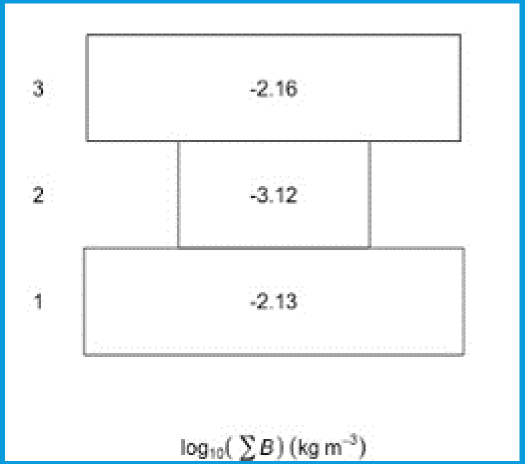
UPSIDE-DOWN PYRAMIDS

- …Secondary production can *exceed* primary production
  - Say what?!

UPSIDE-DOWN PYRAMIDS

- ...Secondary production can *exceed* primary production
  - Say what?!

- This is the "Allen Paradox"
- We saw this in Lab 1!
  - Tuesday Lake Eltonian pyramid: More total biomass in consumer trophic levels than in primary producer trophic level (i.e., suggests more secondary than primary production)



- Stay tuned! The Allen Paradox will be the focus of Lab 3.
  - (Can you solve it???)

UPSIDE-DOWN PYRAMIDS

- …Secondary production can *exceed* primary production
  - Say what?!
- Highly recycled/conserved rates of biomass ingestion efficiency
- Use the same biomass (in different forms) over and over within a community
- In other words, much of secondary production is actually "double-dipping"
- This explains evident "breaking" of the Eltonian pyramid and violation of Lindeman's 10% rule:
  - Rule works (sorta), *IF* not considering turnover/recycling

Note: Stream ecologists like to call it "spiralling" instead of "recycling", because it implies a spatial component as well.

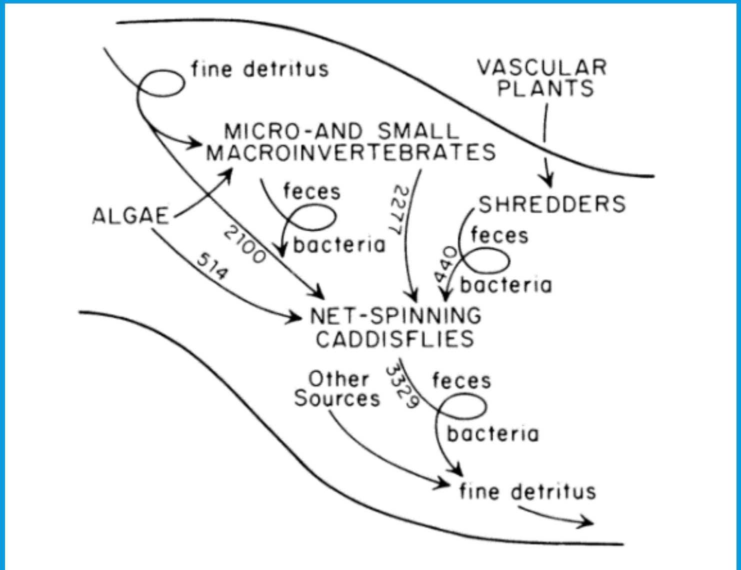


FIG. 2. Role of net-spinning caddisflies in "spiralling" of organic matter in the Tallulah River (all flows in mg dry mass·m^{-2}·yr^{-1}).

Benke & Wallace (1980)